

Spatial variation in the importance of different prey types in the diet of red foxes

Cameron A. Graham^{1,3}, Martine Maron¹, Clive A. McAlpine^{1,2}

¹The University of Queensland, Landscape Ecology and Conservation Group, School of Geography, Planning and Environmental Management, Brisbane, Australia. 4068

²The University of Queensland, The Ecology Centre, Brisbane, Australia. 4068

³Corresponding author email: cam.g.eco@gmail.com

ABSTRACT

Invasive predators are identified as an important threatening process implicated in native species decline and extinction in Australia. This study aimed at developing our understanding of landscape-level spatial patterns in the red fox diet. We established prey importance based on dietary composition of red fox scats, and related this information to landscape structure. The relationship between scat composition and the frequency of detection and spatial patterns of occurrence of small mammals based on survey data from the same region was also evaluated using ordination analyses. We found that native vertebrates, dominated by *Sminthopsinae*, were the most important prey. However, *Mus musculus* were detected significantly more than *Sminthopsinae* across the region. *Sminthopsinae* were detected most frequently in traps in grazing landscapes; however, red fox scats from grazing landscapes were dominated by invertebrates. We propose these patterns may be partially driven by *M. musculus* abundance attracting predation pressure to the landscape and *Sminthopsinae* exhibiting prey naivety resulting in their disproportional representation in red fox scats.

Key words: species response curve; redundancy analysis; spatial processes, threatening processes, prey vulnerability

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Introduction

There is considerable evidence implicating invasive vertebrate predators in the decline and extinction of native species (Pimm 1987; Mellink 1992; Short and Smith 1994; Smith and Quinn 1996; Burbidge and Manly 2002). Due to an absence of co-evolution, native wildlife species are at a disadvantage, often lacking adequate defensive strategies or not recognising invasive predators as a threat (McLean *et al.* 1995; Russell and Banks 2007; Banks and Dickman 2007).

In Australia, the red fox is an important invasive predator that was successfully introduced in 1871 after several failed attempts (Rolls 1969). It is thought that the success of this introduction was due to an earlier establishment of self-sustaining feral European rabbit (*Oryctolagus cuniculus*) colonies, a species that is their preferred prey (Rolls 1969; Jarman 1986; Banks *et al.* 1998). Since then, foxes continued to increase their range in the wake of the rabbit expansion across the continent (Saunders *et al.* 2010). However, foxes are now also successful in landscapes where rabbit densities are too low to support fox populations (Catling and Burt 1995). This demonstrates their relatively quick adaptation to subsidising their diet with native species (Cupples *et al.* 2011). Since their introduction to Australia, the spread of foxes across the continent has coincided with the extinction of many small vertebrates in the critical weight range of 35 – 5000 g (Burbidge and McKenzie 1989; May and Norton 1996).

The diet of red foxes has been studied extensively in Australia (e.g. Martensz 1971; Coman 1973; Wallis and Brunner 1987; Pech and Hood 1998; Molsher *et al.* 2000; Lapidge and Henshall 2001; Holden and Mutze 2002; Glen *et al.* 2006; Hradsky *et al.* 2017). These studies have demonstrated the generalist diet of the red fox and its variation among seasons and in response to fluctuating rabbit abundance. Yet the influence of landscape structure on the spatial dietary patterns of foxes has been largely ignored. One study examined the influence of different habitat patches on the diet of red foxes on a grazing property (Palmer 1995); however, the diet samples were classed by the habitat patch from which they were collected and the influence of the broader neighbourhood within which the fox was potentially foraging was not considered. Knowledge gaps of the patterns among landscape configuration and composition and red fox dietary composition remain. Understanding the spatial variation in red fox diets at a local landscape and regional level can have important implications for conservation management, particularly if there are landscape features that affect red fox predation of native species.

In this study, we investigated the diet of red foxes in agricultural landscapes in the Brigalow Belt South Bioregion, Queensland, where rabbits are at very low densities and thus unlikely to be important in fox diets. We investigated the relative importance of prey groups,

particularly the importance of native compared to introduced vertebrate prey, in the composition of red fox scats. We contrasted this with the detection frequency and spatial analyses of small mammal data from the region. We expected that small mammals detected more frequently in the region would have a higher representation in the composition of red fox scats. We also investigated how scat composition differed among landscapes of varying composition and configuration. As the prevalence of native vertebrates varies depending on habitat extent in the landscape (Holland and Bennett 2009), we expected shifts in the composition of fox diets to occur as landscape characteristics changed, e.g. an increase in the diversity of prey in fox scats with increasing landscape heterogeneity.

Methods

Study region

This study was conducted in the Brigalow Belt South Bioregion (BBS), south east Queensland, Australia (Fig.1). The bioregion lies within the subtropical zone and its climate is characterised by wet and dry seasons with the wettest months occurring during late spring to early autumn (Lloyd 1984). Topography of the bioregion is characterised by low undulating relief dominated by deep cracking clays that once supported extensive brigalow (*Acacia harpophylla*) grassy woodlands (Seabrook *et al.* 2006). However, since the 1960s, the bioregion has experienced a rapid conversion of contiguous woodland

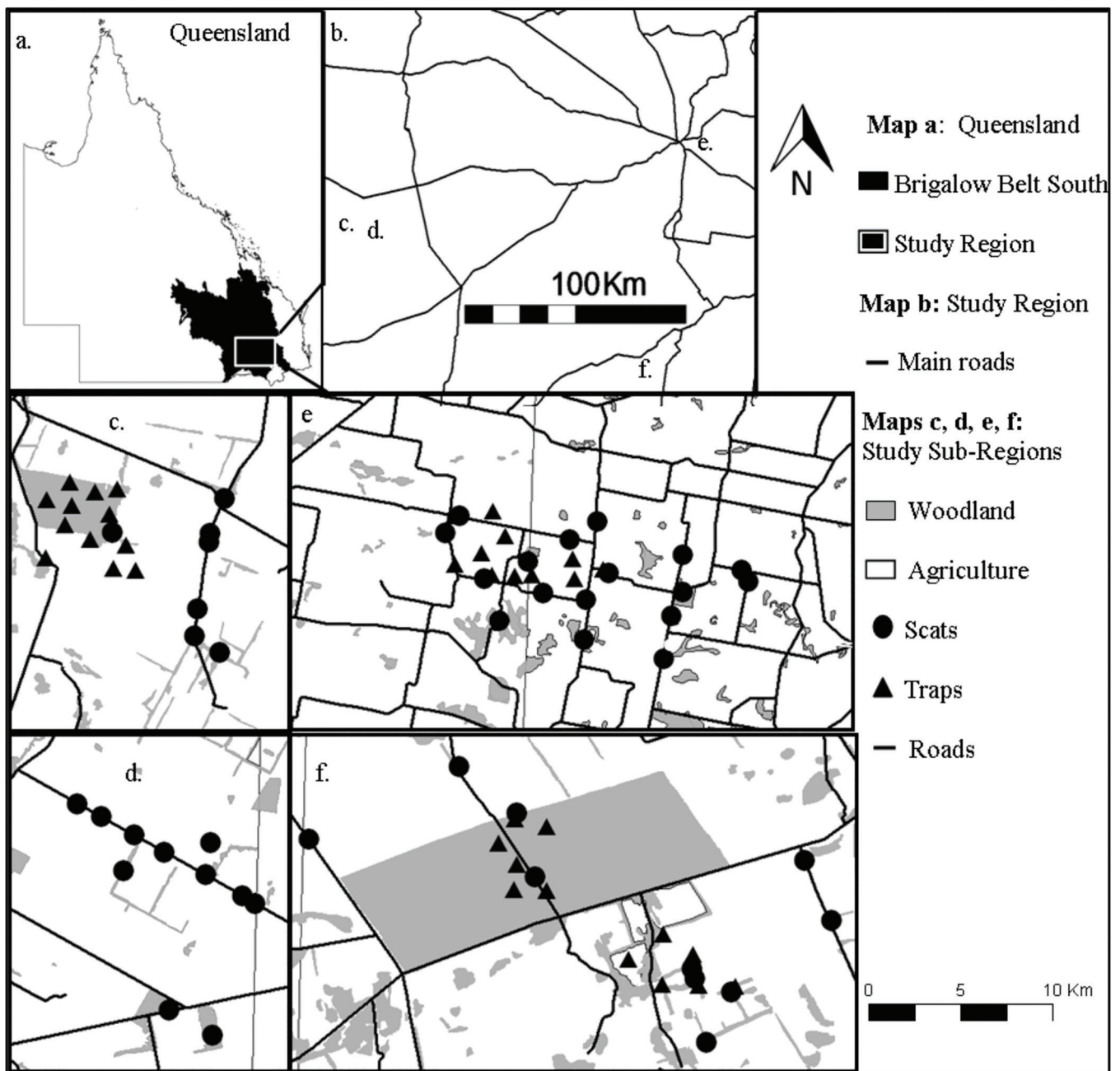


Figure 1. The Brigalow Belt South bioregion, Queensland (a.); study region (b.) and the study sub-regions of: c and d. Meandarra, e. Dalby, f. Moonie, with locations of scat samples and pitfall traps.

landscapes to highly fragmented landscapes dominated by broadscale grazing and cereal crops (Johnson 1980, Seabrook *et al.* 2006). The control of wild dog (*Canis lupus* ssp.) and European rabbit are major agricultural management priorities in the region. An extensive network of rabbit and wild dog fences and continual direct control programs maintain wild dog and rabbit populations at low densities. Further to this, the deep cracking clay soils are unsuitable for rabbit warrens thus further suppressing rabbit abundance (Parer and Libke 1985).

Scat surveys and analyses

Red fox scats were collected during two survey periods. First an intensive search of 62, 1 ha study sites during spring 2008 to early autumn 2009 in the sub-regions of Dalby, Meandarra and Moonie (see Graham *et al.* 2012). Second, scats were opportunistically collected during strategically designed trapping surveys of red foxes during spring 2009 to early autumn 2010 in the same regions (Fig. 1). To avoid sub-seasonal bias among sub-regions, the scat surveys were alternated among the sub-regions on a fortnightly basis. After consultation with local landholders, no fox control programs were known to have been undertaken in the six months prior to or during the scat collection.

Scats were oven dried at 80°C for 48 hours and their dry mass weighed to ± 0.01 of a gram. The macroscopic constituents of each scat were separated into five groups: hair (mammalian), feathers (avian), scales (reptilian), exoskeleton (invertebrate) and vegetation. Mammalian prey was identified using a compound microscope by keying out the cross section, medulla and scale of guard hair samples following Triggs and Brunner (2002). Other macroscopic items were also used for identification, such as skeletal remains. Prey groups were categorised to their lowest identifiable taxonomic level; for example, reptiles were only identifiable to class level, thus 'reptiles' constituted a prey group; whilst mammals were identifiable to genus or species. Species larger than 5 kg were classed as carrion as species larger than this are considered less vulnerable to fox predation (Burbidge and McKenzie 1989).

Prey importance

Frequently-consumed small prey can potentially cause misleading interpretations of their importance in the diet of predators (Floyd *et al.* 1978). It is therefore recommended that the frequency of occurrence and biomass are both presented (Klare *et al.* 2011). Other issues that may also lead to misinterpretations of scat analyses include effects of the ratio of indigestible to digestible material and the rate at which indigestible material moves through the digestive tract of a predator (Klare *et al.* 2011). For example, when consuming large carrion, such as macropods, red foxes may avoid consuming indigestible material such as hair, whereas when consuming small prey species (e.g. *M. musculus*), indigestible material is unavoidable. Also, the frequency

of individual animals from the same prey group in one scat could be estimated by the number of bones that identify a single animal, e.g. mandibles. However, we found that many scats that contained hair from small prey species contained very few or no skeletal fragments (Triggs *et al.* 1984) whilst occasionally a scat contained bones from two or possibly more individuals. This indicated that different types of indigestible material (e.g. bone and hair) do not pass through the digestive tracts of foxes at the same rate. Thus, reliable identification of how many individuals of the same prey group occurred in each scat was not possible (Floyd *et al.* 1978; Klare *et al.* 2011). Prey groups were thus recorded as being present in a scat. Groups that did not contribute more than 5% to the total mass of scats were omitted from the analyses examining the influence of landscape composition and configuration.

We explored if the representation of prey groups in scats varied among sub-regions which may affect interpretability of the results. We used analysis of variance to compare the mass of prey items in each prey category among sub-regions, sampling period and an interaction of the terms. Analyses of variance were conducted using Statistica v. 10 (StatSoftInc, 2011)

All prey groups were ranked by calculating an index of relative importance (IRI) for each one. The IRI for each prey group is calculated using the formula:

$$IRI = F(N+M)$$

where F = percentage of prey group presence of the total presence of prey items among scats (Frequency %), N = percentage of scats in which the prey item was present (Prey %) and M = percentage of total mass of all scats (Pinkas 1971; Martin *et al.* 1996). Biases toward more frequently taken or larger prey can be introduced by only presenting the proportions of frequency or mass. Calculating the IRI can reduce these biases and allow more meaningful ecological interpretations to be made (Martin *et al.* 1996).

Landscape covariates

An earlier study of fox movement patterns had revealed that the mean width of a red fox home range in the regions of Dalby, Meandarra and Moonie in the BBS to be approximately 3 km (C. Graham unpublished data, Lunney *et al.* 2002). The mean width of home ranges was used as a buffer distance to delineate the landscape where the fox likely obtained its food directly related to each scat sample (Lunney *et al.* 2002). The landscape characteristics were measured within this buffer distance surrounding each diet sample (Table 1). Land cover within the 3-km diameter landscapes was categorised as cropland, grazing land or woodland (Table 1). Site-level habitat attributes were not considered for the diet analysis because the exact location from which the prey were taken was not known.

Land cover was mapped using SPOT5 satellite imagery at a multispectral resolution of 10 m, panchromatic at 5 m, using ArcGIS v.9.3 (ESRI 2004). Landscape scale variables were calculated using FRAGSTATS software (v.3.3, McGarigal *et al.* 2003) at a 5-m cell resolution. Site scale vegetation data was provided by C.A. McAlpine as part of the vegetation survey component of the Restoration of Fragmented Brigalow Landscapes for Conservation ARC Linkage Project (RFBLC).

Spatial variation in diet

We used multivariate ordination to examine the influence of landscape composition and configuration on prey mass within each prey category that contributed >5% mass to red fox scats. A direct gradient analysis was used to examine how each prey group's proportional contribution to the mass of each fox scat varied among landscapes of differing composition and configuration. Selection of ordination method was determined by conducting a detrended correspondence analysis (DCA). This analysis determines the length of the compositional gradient (ter Braak and Smilauer 2002), which can indicate the most appropriate ordination analysis method. A long gradient of >4 indicates a unimodal response and a short gradient of <3 indicates a linear response (ter Braak 1995; Leps and Smilauer 2003). The result of the DCA (gradient length = 2.9), indicated that a redundancy analysis (RDA) was the most appropriate ordination method (ter Braak and Smilauer 2002). An RDA analysis is a constrained form of a linear principal components analysis and is analogous to a multivariate multiple regression. However, the predictor (environmental) variables are constrained to linear composites (canonical variates) for each axis, reducing the number of parameters in the regression. The goal is to provide canonical coefficients (weights) that best explain the relationship between the response and the predictors in the canonical variates (Leps and Smilauer 2003). Forward selection of predictor variables provides additional information on the importance of the predictor variables, allowing them to be ranked by order of importance (ter Braak and Smilauer 2002). Significance of variables was determined by using 499 unrestricted Monte Carlo permutations.

To improve model instability, we calculated 95% confidence intervals of the overall scat mass and for each prey group. Prey groups with a mean mass lower than the lower bound of the overall prey mass of fox scats confidence interval were removed from the analysis. To further avoid bias towards species with a lower contribution, response variables were standardised by the error of variance not explained by the predictor variables, where the inverse of the error is used to weight the response (Leps and Smilauer 2003). This method provides greater weight to species better described by the predictor variables in the analysis (ter Braak and Smilauer 2002).

To reduce the number of predictor variables in the RDA, predictors were first selected for their strength of correlation

with individual prey groups ($r \geq 0.15$). Collinearity among predictor variables was then investigated by first inspecting a Pearson correlation matrix, identifying variables with high correlations ($r > 0.5$), and high variance inflation factor in initial analyses ($VIF > 10$). Predictor variables with high correlations and VIF can be considered proxies of one another and can lead to model instability requiring one of the variables to be removed. To retain the most appropriate variables, the strength of Wilks' lambda values in initial analyses and their ecological interpretability were used to determine their suitability for the final analyses (Leps and Smilauer 2003). Predictor variables selected for the final analysis included: fractal dimension of patches ('Shape'), landscape contagion ('Contagion'), woodland large patch index ('WoodLPI'), cropland large path index (CropLPI), the number of grazing patches ('GNP'), woodland aggregation of like habitat ('WoodAgg'), total area of grazing land ('Graze'). All predictor variables were standardized to a mean of 0 and variance of 1. *Post hoc* variance partitioning was conducted to determine the amount of variance explained by each predictor variable for the first two axes and the overall shared variation (Leps and Smilauer 2003).

Species response curves were then constructed to determine the mode of the response of prey groups (linear or unimodal) against complex environmental gradients of the first two RDA axes. This analysis fits a multivariate general linear model to estimate the importance of each axis for each prey group based on Akaike's Information Criterion (AIC).

We conducted a Shannon's Diversity Index analysis fitted with quadratic function. The index can be roughly interpreted as equal diversity of species given equal abundance. An attribute plot summarizing the diversity and evenness of prey groups per scat for the first two axes of the RDA was constructed using a fitted regression model with a quadratic (GLM smoother). All analyses were computed using CANOCO v. 4.5 (ter Braak and Smilauer 2002).

Sampling effort

Sample-based rarefaction curves were calculated to determine if sample size were adequate (Heck *et al.* 1975). The proportion data were treated as incidence of prey among scats (i.e. presence/absence) and calculated using the 'classic Chao 2' estimator with 100 randomizations in 'EstimateS v.9' (Chao *et al.* 2009; Colwell and Elsensohn 2014). The sample-based rarefaction curve was calculated at the regional and sub-regional level for prey that contributed >5% of mass to the total mass of scats. Survey effort is deemed to be adequate when the accumulation of prey groups reaches an asymptote and the unconditional confidence interval envelope closes (Colwell *et al.* 2012). The same procedure was applied for determining sampling effort for the small mammal prey surveys described below using presence/absence of species detections at each trap site and used to justify if prey species need to be pooled for more robust analyses.

Small mammal prey surveys

The small mammal prey data were from a separate dataset collected in same study regions and seasons as this study (McAlpine *et al.* 2015). The dataset was used to analyse the frequency of detections and spatial distribution of small mammal prey species in the study region. The survey consisted of 36 survey sites within the three regions (12 per region) in this study. Surveys were conducted from spring 2008 to autumn 2009. Detailed survey methods are in McAlpine *et al.* (2015).

Small mammal frequency of detection analysis

A comparison of means of the frequency of detection of small mammals was conducted to confer the interpretation of the IRI analysis. An exploratory analysis of the small mammal data indicated a non-parametric distribution with several ties and zero values. To account for violation of t-test assumptions and the effect of zeroes and ties in a Wilcoxon Signed Rank test, a Wilcoxon-Pratt Signed Rank Test was used to analyse the frequency of detections among introduced and native small mammal species (Pratt 1959). We used Kruskal-Wallis test to explore the variation of the frequency of detection of introduced and native small mammal species among the three

study sub-regions. This was applied to detect significant regional prey distribution patterns which may affect the interpretation of the frequency of detection results.

Small mammal spatial distribution analysis

We applied the same procedures as the diet analysis for conducting multivariate ordination analysis and selection of predictor variables. The result of the DCA (gradient length = 1.5), indicated that a redundancy analysis (RDA) was the most appropriate ordination method (ter Braak and Smilauer 2002). Predictor variables selected for analysis were: proportion of landscape covered by Woodland (Wood), Grazing and Cropping; Contagion; Patch Age; Patch Width and Shrub Density (Shrub) (Table 1).

Results

Prey importance

A regional flood inundated the study landscapes and persistent flood water reduced the access and time allowed for field data collection. However, 46 red fox scats were collected with a mean weight of 9.33 g (s.e. = 2.76 g) with 102 identified occurrences of prey items. Native

Table 1. The classification, units of measurement and description of landscape and land cover type (woodland, grazing and cropping) and habitat attributes to explain spatial variation of the composition of red fox scats and small vertebrate spatial distribution analysis.

Analysis	Variable	Description
Landscape scale		
Prey and Diet	Total area	Percentage of area covered by land cover type: woodland, grazing, cropping.
Prey and Diet	Large patch index	Percentage of area of the largest patch for each land cover type in the landscape
Prey and Diet	Number of patches	Number of disjunct patches in the landscape and for each land cover type
Prey and Diet	Patch density	Number of patches per 100 hectares
Prey and Diet	Aggregation of 'like' habitats	A measure of habitat type 'clumpiness' where 0 = maximal disaggregation to 100 = the habitat type occupies the entire landscape.
Prey and Diet	Fractal dimension of patches	Fractal dimension of land cover type patches where 1 = simple to 2 = highly complex shapes.
Prey and Diet	Contagion	Measure of 'clumpiness' of like patches and edge density in a 1 km buffer surrounding each site.
Habitat Site Scale		
Prey	Patch width	Average width of patch measured in metres using PolygonWidth.bas macro
Prey	Patch age	Estimated age of remnant patch using historical aerial photography
Prey	Shrub density	Proportion of site covered by shrubs in one hectare surrounding per trap site.
Prey	Ground cover	Proportion of ground cover types: grass, forbs, litter and bare. Measured in 1 m ² quadrats located every 10m along 50m transect per trap site.
Prey	Large tree density	Average density of large (> 100 cm DBH) trees in one hectare pre trap site

vertebrates contributed the greatest proportion of mass to red fox scats (mean proportion = 0.38, s.e. = 0.06) and *M. musculus* contributed the greatest proportion of mass for any prey group at genus/species level (mean proportion = 0.18, s.e. = 0.05) (Fig. 2). We identified five prey groups that's mean mass was within the overall mass 95% confidence interval (Table 2). Of the five prey groups, there were no significant differences in the frequency or mass of prey categories among sampling periods or regions (Table 3). The IRI indicated that native vertebrates as a group (IRI = 6640.0), excluding carrion, were more than twice as important as the next most important prey type, invertebrates (IRI = 2839.7) (Table 3). Separating vertebrates into native and introduced mammals, birds and reptiles, we found native mammals (IRI = 2290.7), excluding carrion, were the most important (Table 3). At the taxonomic level of species, *Mus musculus* (IRI = 1056.9) was the most important prey group (Table 4).

Spatial variation in diet

For prey groups included in the analysis the first axis of the redundancy analysis explained 19.7% of the variation and the second axis explained 8.3% (31% total 4 axes). The redundancy analysis indicated that landscape composition and configuration significantly influenced the dietary composition of foxes (axis 1 = $p < 0.01$, all four axes = $p < 0.01$). Partitioning of explained variance of all axes showed variance explained by each predictor variable as follows: GrazeNP 12.5%, CropLPI2%, Contagion 2%, Shape2%, WoodLPI 1.5%,

Table 2. 95% mean and confidence intervals of the overall scat mass and for each prey group. Prey groups indicated * have a mean mass weight lower than the 'Overall' lower confidence interval and were excluded from further analyses.

Species	Mean	Lower	Upper
Overall	1.03	0.80	1.27
Carrion	1.25	0.36	2.16
Invertebrate	2.09	1.18	2.99
Vegetation	0.28*	0.03	0.54
<i>Sminthopsis</i>	1.93	1.04	2.83
Bird	1.02	0.35	1.69
Reptile	0.19*	0.07	0.32
<i>M. musculus</i>	1.69	0.76	2.62
Lagomorph	0.41*	0.00	0.85
Incidental	0.48*	0.00	1.05

WoodAgg 1.5% (shared variance 9.5%). Patterns of dietary composition from the RDA showed that the mass of *Sminthopsis* and *M. Musculus* in red fox scats increased in landscapes with more contiguous woodland and cropland (Fig. 3). Carrion had a strong linear relationship with mixed use landscapes dominated by grazing patches (Fig. 3). The proportion of bird mass in the scats of red foxes was also related to landscapes heterogeneity with a greater emphasis on edge density (Fig. 3). The mass of invertebrates increased and the overall mass of vertebrates decreased in scats in more homogeneous grazing landscapes (Fig. 3).

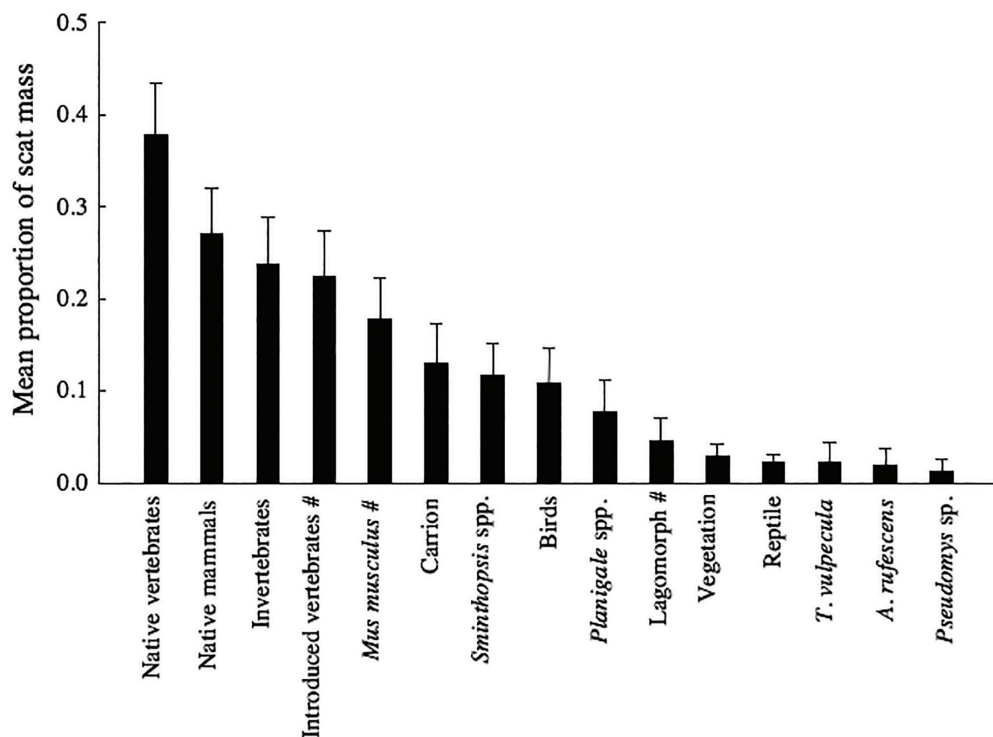


Figure 2. Mean (+/- s.e.) proportion of scat mass contributed by each prey category. Number of fox scats = 46, total prey occurrences = 102, total mass = 481 g. Abbreviated prey species: *M. Musculus* (*Mus musculus*), *T. vulpecula* (*Trichosurus vulpecula*) and *A. Rufescens* (*Aepyprymnus rufescens*). # indicates introduced mammals.

Table 3. Analysis of variance on the representation of prey mass among subregions, year of study and interaction of subregion*year.

Prey group	Mass					
	Subregion (d.f. = 2)		Year (d.f. = 1)		Subregion*Year (d.f. = 2)	
	F	p	F	p	F	p
Invertebrate	0.74	> 0.05	1.52	> 0.05	0.41	> 0.05
<i>M. musculus</i>	1.18	> 0.05	2.53	> 0.05	0.35	> 0.05
Carrion	0.70	> 0.05	0.23	> 0.05	0.47	> 0.05
<i>Sminthopsinae</i>	0.25	> 0.05	0.24	> 0.05	0.43	> 0.05
Bird	1.71	> 0.05	2.76	> 0.05	1.84	> 0.05

Table 4. Importance of prey groups based on 102 prey items identified from 46 scats. Prey groups considered in the analysis are ranked based on the index of relative importance (IRI).

Rank	Prey	Number	Mass %	Number %	Frequency %	IRI
1	Invertebrates	27	21.9	26.5	58.7	2839.7
4	Carrion	11	13.0	10.8	23.9	569.9
7	Vegetation	6	3.0	5.9	13.0	115.6
	Native vertebrates	39	40.1	38.2	84.8	6640.0
2	<i>Sminthopsinae</i>	17	21.3	16.7	37.0	1403.1
5	Bird	10	10.7	9.8	21.7	445.4
6	Reptile	9	3.1	8.8	19.6	232.8
9	Incidental prey	3	5.1	2.9	6.5	52.3
	<i>T. vulpecula</i>	1	2.0	1.0	2.2	6.5
	<i>A. rufescens</i>	1	1.8	1.0	2.2	6.0
	<i>Pseudomys</i> sp.	1	1.3	1.0	2.2	4.9
	Introduced vertebrates	19	22.0	18.6	41.3	1678.1
3	<i>M. musculus</i>	15	17.7	14.7	32.6	1056.9
8	Lagomorph	4	4.3	3.9	8.7	71.2

The general linear modelling of the species response curves determined that the response of prey groups to the complex environmental gradients of axes 1 and 2 were significant. The mass of prey groups in fox scats significantly associated with axis 1 included carrion ($F = 35.5$, $p = <0.01$), bird ($F = 4.9$, $p = <0.05$) and invertebrate ($F = 6.4$, $p = <0.05$) (Fig. 3). The mass of prey groups in fox scats significantly associated with axis 2 included *Sminthopsinae* ($F = 9.0$, $p = <0.01$), *M. musculus* ($F = 5.1$, $p = <0.05$) and invertebrate ($F = 11.1$, $p = <0.01$) (Appendix A).

The attribute plot of the RDA implied that diversity of prey items and their evenness in abundance in fox scats significantly increased with increasing contiguity of woodland and increased interspersed of land cover types ($F = 2.69$, $p = <0.05$). As landscapes become more homogeneous (increasing contagion) dominated by grazing land, prey diversity decreased (Fig. 4).

Sampling effort

The sample based rarefaction curve analysis indicated that the sample size for the six most important prey groups analysed was adequate, at the regional level reaching an asymptote at the 19th sample and the

unconditional confidence interval envelope closing at the 40th sample; at the sub-regional level asymptotes were met (Appendix B). If testing for the entire prey set (12 prey types) that included three prey types that only occurred once, the sample size would have been inadequate as it did not reach an asymptote at the regional and sub-regional level; this may be a product of the opportunistic nature of red foxes when foraging and their generalist diet (Appendix B).

For the following analysis of sampling effort for prey detections among traps, the rarefaction curves indicated that a more robust analysis was achieved by pooling *Sminthopsinae* (Appendix C). At the regional level using un-pooled *Sminthopsinae* as it did not reach an asymptote. With pooled *Sminthopsinae* at a sub-regional level, an asymptote was reached by the 8th sample and the confidence interval envelope closing by the 10th sample.

Prey frequency of detections

The pitfall trap surveys detected 107 incidents of 6 identified small mammal species: introduced *M. musculus*, and native *Planigale gilesi*, *P. maculata*, *P. tenuirostris*, *Sminthopsis macroura*, *S. murina*, and an unidentified species of planigale. The non-native *M. musculus* were

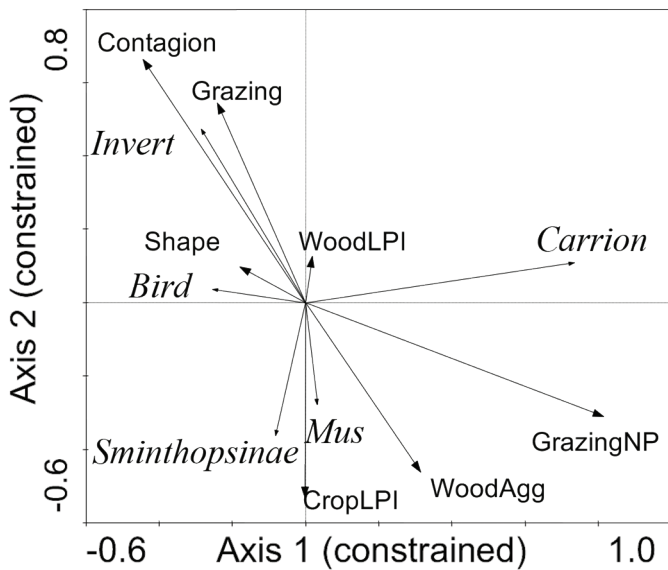


Figure 3. Redundancy analysis triplot of red fox scat composition against landscape predictors. Points indicate ordination of samples. Decreasing angle between arrows and axes indicate increasing correlation of the variable with the axis. The lengths of arrows indicate the importance of the variable. Variable codes: *Mus musculus* ('Mus'), fractal dimension of patches ('Shape'), landscape contagion ('Contagion'), number of grazing patches ('GrazingNP'), the number of grazing patches ('GNP'), Crop Large Patch Index ('CropLPI'), Woodland Large Patch Index ('WoodLPI'), aggregation of woodland patches ('WoodAgg') total area of grazing land ('Grazing') and total area of woodland ('Wood').

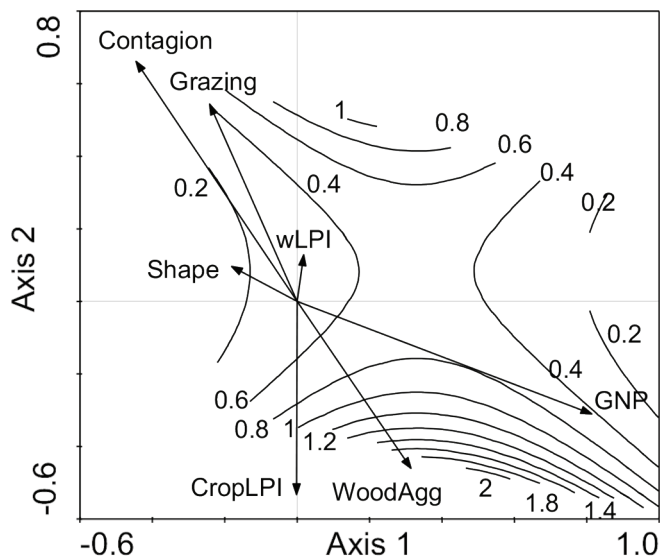


Figure 4. Shannon's Diversity Index of red fox scats attribute plot. Contours indicate diversity of prey groups in scats against axes 1 and 2 of the RDA which was significant ($F = 2.69, p = <0.5$). Decreasing angle between arrows and axes indicate increasing variable correlation with the axes. The lengths of arrows indicate their importance. Variable codes: fractal dimension of patches ('Shape'), landscape contagion ('Contagion'), the number of grazing patches ('GNP'), total area of grazing land ('Grazing'), large patch index of crops ('CropLPI'), large patch index of woodland ('WoodLPI') and aggregation of wood patches ('Woodagg').

detected significantly more frequently comprising 83% of detections (Wilcoxon-Pratt Signed-Rank Test $z = 4.9824, p < 0.001$) (Fig. 5) and were detected at every trap site ($\mu = 2.47, \text{s.e.} = 0.2$). *Sminthopsis* and *Planigale* species were pooled into their sub-family 'Sminthopsinae' due to the low number of each species detected. *Sminthopsinae* were detected at 13 trap sites ($\mu = 0.5, \text{s.e.} = 0.13$) across the sub-regions. *Sminthopsinae* showed no significant variation among sub-regions ($F = 0.4, \text{d.f.} = 2.33, p = 0.05$) (Fig. 6), *M. musculus* did show significantly less detections in the sub-region Meandarra ($F = 6.3, \text{d.f.} = 2.33, p < 0.05$) (Fig. 6); however, the detection frequency of *M. musculus* in the sub-region Meandarra was still significantly higher than *Sminthopsinae* ($z = 2.4, p < 0.05$).

The RDA analysis of the spatial variation of *M. musculus* and *Sminthopsinae* explained 24.6% on the first axis and 8% on the second axis (32.6% total two axes) (Fig. 7). The redundancy analysis under the full model indicated that landscape and site scale habitat attributes significantly influenced the detection frequency of small mammals on the first axis ($p = < 0.05$) and was associated with *Sminthopsinae* ($F = 11.76, p < 0.01$) (Fig. 7). The second axis was overall shown not to be significant ($p > 0.05$); however, *M. Musculus* was significantly associated with axis two ($F = 7.84, p < 0.01$). Partitioning of explained variance of all axes showed variance explained by each predictor variables: Grazing (4.4%), Cropping (1%), Shrub (7.9%), Contagion (1%), Wood (2%), Patch age (3.6%), Patch width (3.3%) and shared variance (9.4%). The RDA analysis showed a strong relationship of *Sminthopsinae* and grazing landscapes (axis 1) (Fig. 7). The density of shrubs was important in driving detections of both *Sminthopsinae* and *M. musculus* at a site scale. *M. musculus* were more likely to be detected in narrow patches and older remnant woodland patches than *Sminthopsinae* (axis 2) (Fig. 7).

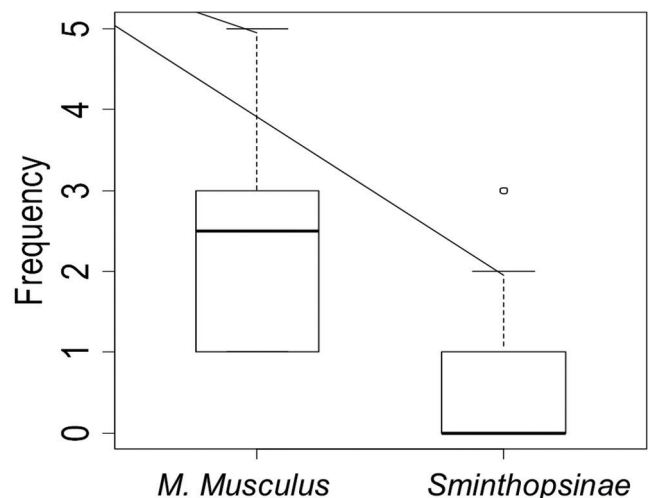


Figure 5. Wilcoxon-Pratt Signed Rank Test of the frequency *M. Musculus* and *Sminthopsinae* prey detected in traps in the BBS study region.

Discussion

This study indicated that in the Brigalow Belt South Bioregion, where rabbits are scarce, small native mammal species were more vulnerable to fox predation in landscapes where introduced *M. musculus* were more abundant. These patterns were partially explained by landscape composition and configuration, with small native mammals more likely to occur in scats collected in more heterogeneous landscapes with higher abundance of introduced small mammals.

Our study further supported the global observation of red foxes having a wide, omnivorous diet (Cook and Hamilton 1944; Palmer 1995; Goldyn *et al.* 2003; Saunders *et al.* 2004) and that mammals are highly important prey (Coman 1973; Palmer 1995; White *et al.* 2006). However, novel aspects of their diet in the study region were observed, such as the greater importance of small native mammals compared to small introduced mammals.

Scat composition and prey detection

The composition of fox scats showed that native vertebrates, especially small native mammals, e.g. *Sminthopsinae* occurring in 37% of scats, were the most important prey detected in red fox scats. Studies have shown low rates of predation on small native mammals where rabbits occur are common (Coman 1973; Cupples *et al.* 2011); however, opportunistic predation on less common and rare species can have significant impacts (Coman 1973; Short 2002). In regions where rabbit populations have declined, the predation response by red foxes can be highly variable, but typically exhibit a Type III functional response which is driven by prey abundance (Holling 1959; Cupples *et al.* 2011). Among the study regions, *M. musculus* were detected three to eight times more frequently than *Sminthopsinae*;

however, *Sminthopsinae* were detected more frequently in red fox scats. In contrast to the expected Type III functional response, it appeared that *Sminthopsinae* were disproportionately represented in the diet of red foxes. The reason for the high representation of *Sminthopsinae* detected in red fox scats remains unclear.

Invertebrates are often considered an important supplementary prey group for red foxes (Molsher *et al.* 2000) particularly where rabbits are scarce (Paltridge 2002). Seasonal shifts in their frequency of occurrence in the diet of red foxes are also commonly reported, with predation increasing during summer or when preferred prey species populations are low (Croft and Hone 1978; Lunney 1990; Palmer 1995; Holden and Mutze 2002). This may explain the high frequency of invertebrates detected in red fox scats during this study, which was conducted from spring to autumn.

Carrion was an important component of red fox scats occurring in 20% of samples. It is a common and often important supplementary prey item for red foxes (Catling 1988; Holden and Mutze 2002), and has been found to compose more than 60% of a red fox diet (Palmer 1995). Types of carrion detected in this study included cattle (*Bos* spp.), feral pig (*Sus scrofa*), kangaroo and wallaby (*Macropus* spp.). In the study region, carrion was commonly observed in the field as road-kill; less commonly seen were dead livestock and parts of game animals (e.g. macropods and feral pig) left from processing in the field by commercial game harvesters (May and Norton 1996; Lapidge and Henshall 2001). In contrast to our study and others (e.g. Coman 1973; Palmer 1995; Mitchell and Banks 2005), Cupples *et al.* (2011) detected a low frequency of carrion in red fox scats in the Simpson Desert where livestock is absent and human activity is scarce. This suggests that a considerable amount of carrion is a product of human activity (Martensz 1971; Lapidge and Henshall 2001,

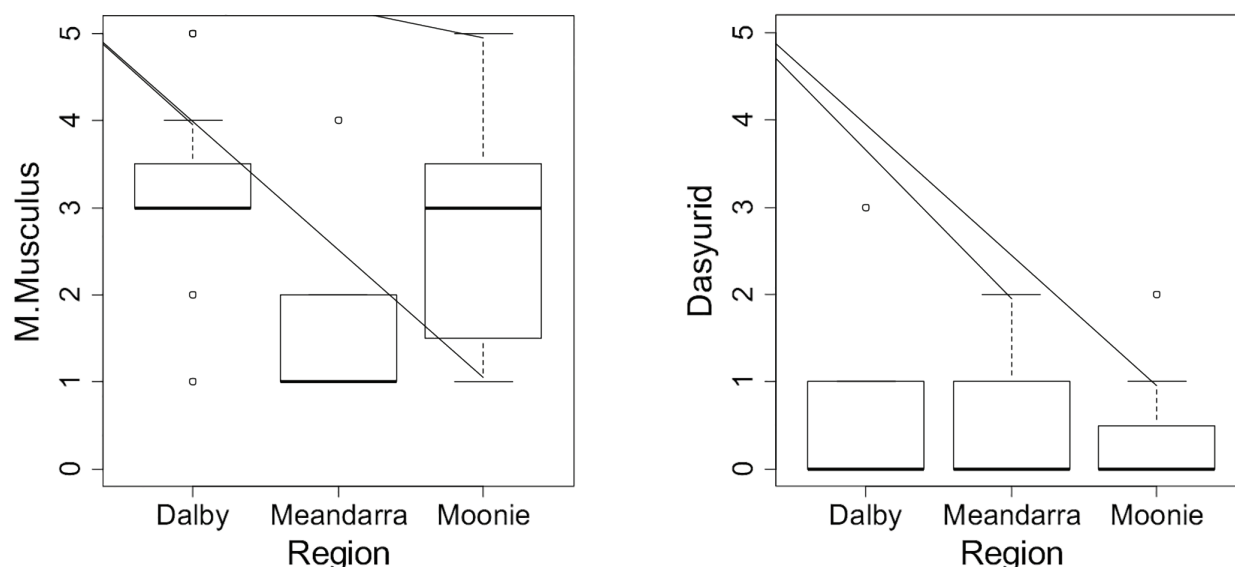


Figure 6. Kruskal-Wallis test of the means of the frequency of detection of *M. musculus* and *Dasyurid* (*Sminthopsinae*) among sub-regions.

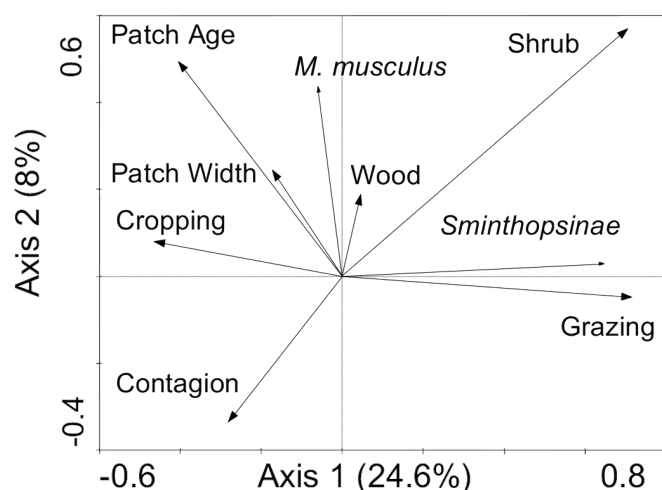


Figure 7. Redundancy analysis triplot of *M. Musculus* and *Sminthopsinae* detections against landscape predictors. Points indicate ordination of samples. Decreasing angle between arrows and axes indicate increasing correlation of the variable with the axis. The lengths of arrows indicate the importance of the variable. Variable codes: landscape contagion ('Contagion'), grazing coverage ('Grazing'), broadscale cropping coverage (Cropping); woodland landscapes (Wood); shrub density (Shrub); remnant patch width (Patch Width); remnant patch age (Patch Age).

DeVault *et al.* 2011). The proportion of the mass of carrion in the fox scats may have been underestimated in this study, as it is likely that a fox will consume a greater ratio of digestible than indigestible material (Klare *et al.* 2011).

Spatial variation in red fox diet and small mammal detections

Our study demonstrated that the composition of red fox scats significantly varied among different landscapes in the same bioregion. Diversity and frequency of prey groups, especially small mammals, in scats increased in more heterogeneous landscapes whereas scats in more homogeneous grazing landscapes were dominated by invertebrates. Studies across different regions in Australia have shown a mixed response of small mammal species abundance to grazing intensity, for example rodents have been shown to have a strong positive response to cessation of intensive grazing. *Sminthopsinae* populations, however, have been shown to have little to no change in response to the cessation of grazing, although their abundance is typically low across landscapes compared to rodents (Read and Cunningham 2010; Legge *et al.* 2011; Waudby and Petit 2015).

We observed the introduced rodent *M. musculus* were associated with complex landscapes and *Sminthopsinae* were associated with grazing landscapes. In both cases shrub density in the landscape was an important positive factor providing cover and for *Sminthopsinae* deep cracks in clay soils, which is a dominant feature in these landscapes, are also extensively used for cover (Warnecke *et al.* 2012). Red foxes in the region have also been shown to have elevated activity levels in and around habitats with dense vegetation

(≤ 1.5 m) (Graham *et al.* 2012) presumably for foraging.

Increased foraging opportunities for *M. musculus*, such as seed, invertebrates and leaf matter, in complex landscapes may contribute to the delineation of detection frequency of this species among landscapes. The delineation of *Sminthopsinae* detection frequency, which are insectivores, among landscapes is less clear as essential cover is available across all study landscapes and, although data on the abundance of invertebrates was not available, it was expected that variation of the abundance of invertebrates among landscapes to be negligible.

To explain the over representation of *Sminthopsinae* in red fox scats in landscapes with a significantly higher detection rate of *M. musculus* we hypothesise the overall higher detection frequency of small mammal species in complex landscapes elicited a predatory response in red foxes to focus on small mammals. However, native species can demonstrate prey naivety when exposed to invasive predators, such as not recognising predator scents, making them more vulnerable than species that have co-evolved with predators, such as *M. musculus* and red foxes (Dickman and Doncaster 1984). Shrews, an insectivore, have been shown to be attracted to fresh predator scats which attract beetles despite risk of predation (Dickman and Doncaster 1984). Russel and Banks (2007) have suggested that small marsupial insectivores, may also be attracted to fresh predator scats which attract invertebrates and in turn increasing their exposure to predators.

In contrast, grazing landscapes had an overall lower detection frequency of small mammals despite the higher frequency of detection of *Sminthopsinae*. It is hypothesised that the abundance of a prey group must reach an undefined threshold for prey switching to occur (Boutin 1995). Generalist predators, such as red foxes, will switch to, or focus on the prey group which offers maximum reward for search and handling effort (Boutin 1995). So, despite the perceived higher abundance of *Sminthopsinae* in grazing landscapes, the overall density of small mammals was too low to elicit a functional response and it was more beneficial for red foxes to focus on invertebrates which offered greater return for effort.

Studies have shown that moderate to high grazing intensity can have significant impacts on small mammal diversity and abundance by severely degrading the quality of ground cover and soil compaction (Legge *et al.* 2011). However, grazing impacts appear to be less pronounced for *Sminthopsinae*, especially in landscapes with deep-cracking clay soil. Also, the presence of cracking clays provides cover for small mammals mitigating the impact of grazing on ground cover (Read 1987b). However, this study indicated that even though small native mammals were more frequently preyed upon in complex landscapes, their frequency of detection was higher in grazing landscapes. We assume from the results that in complex landscapes, the high abundance of *M. musculus*

elicits a predatory response in red foxes to focus on small mammals and due to prey naivety, small native mammals are more frequently caught potentially suppressing their abundance in these landscapes. Further to this, the higher abundance of *Sminthopsinae* detected in grazing landscapes is still not high enough to elicit the same predatory response in red foxes but the abundance of invertebrates is. This could explain the high occurrence of invertebrates and low occurrence of small mammals in red fox scats in grazing landscapes. However, these assumptions require further research to confirm whether: the abundance of *M. musculus* and invertebrates trigger predator responses; trapability and habitat preference of *Sminthopsinae* is similar among landscapes and the role of grazing intensity in the region.

Management implications

Heterogeneous landscapes have been found to have a higher probability of red fox activity than more homogenous agricultural or native habitat landscapes (Graham *et al.* 2012). This maybe a result of the higher detection frequency of *M. musculus* in heterogeneous landscapes. In this study, the preferred landscape of *Sminthopsinae* is unknown as, although they are more likely to be detected in grazing landscapes, their populations may be suppressed by invasive predators in agricultural landscapes with higher woodland cover. Increasing native woodland cover in agricultural landscapes could increase red fox predation on native species (Pita *et al.* 2009; Arthur *et al.* 2010); although careful landscape design could mitigate this. Landscape restoration for conservation should aim to minimise edge density in the landscape to avoid producing ecological traps (Yahner 1988).

The manipulation of important food resources in a landscape has been identified as a potential indirect control method for the management of invasive predators (Barlow and Norbury 2001). The impact of the reduction of food resources has been demonstrated by the substantial reduction of red fox abundance after a dramatic reduction in the numbers of rabbits caused by haemorrhagic disease (Holden and Mutze 2002; Robley *et al.* 2004). Strategies developed to manipulate food resources in regions of low rabbit abundance, such as the appropriate removal of dead livestock and road kill, i.e. carrion, may also significantly impact the red fox populations. The aforementioned indirect control methods could produce a spike in red fox predation on native fauna as they try to meet their nutritional requirements (Norbury 2001; Robley *et al.* 2004), but the level of predation would be expected to decrease as red fox abundance relaxes to the carrying capacity of the managed landscape (Holden and Mutze 2002). To counter the immediate impact of fox predation on native species, direct red fox control effort could be applied to reduce fox abundance in the short-term (Norbury 2001).

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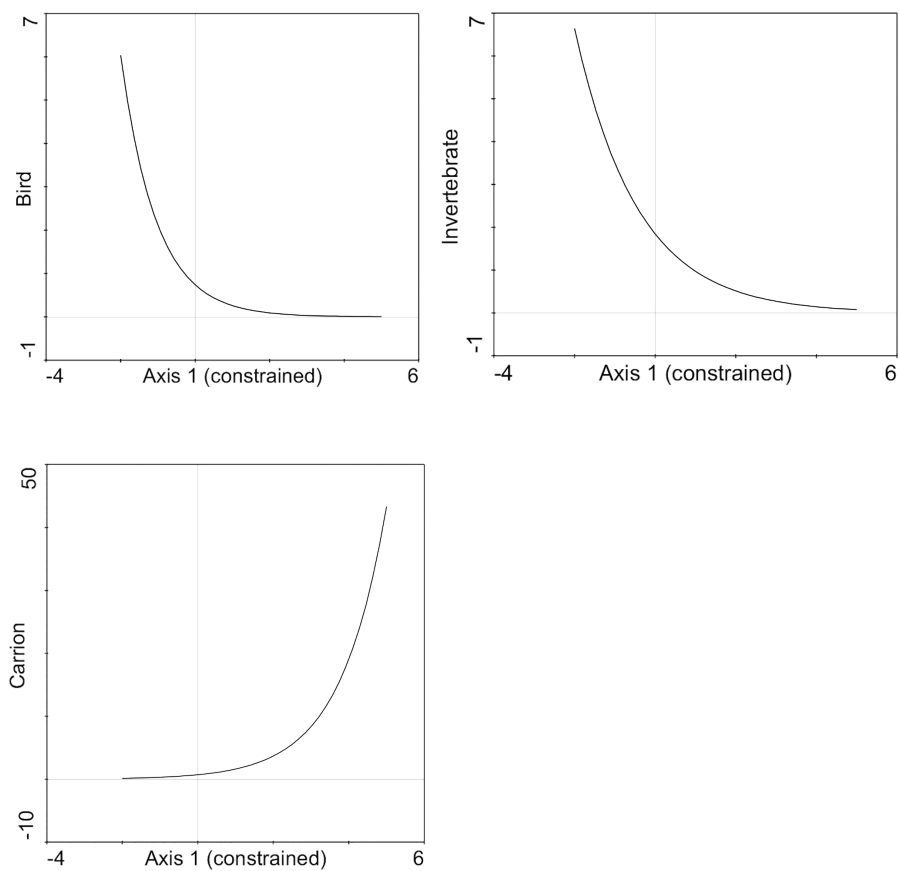
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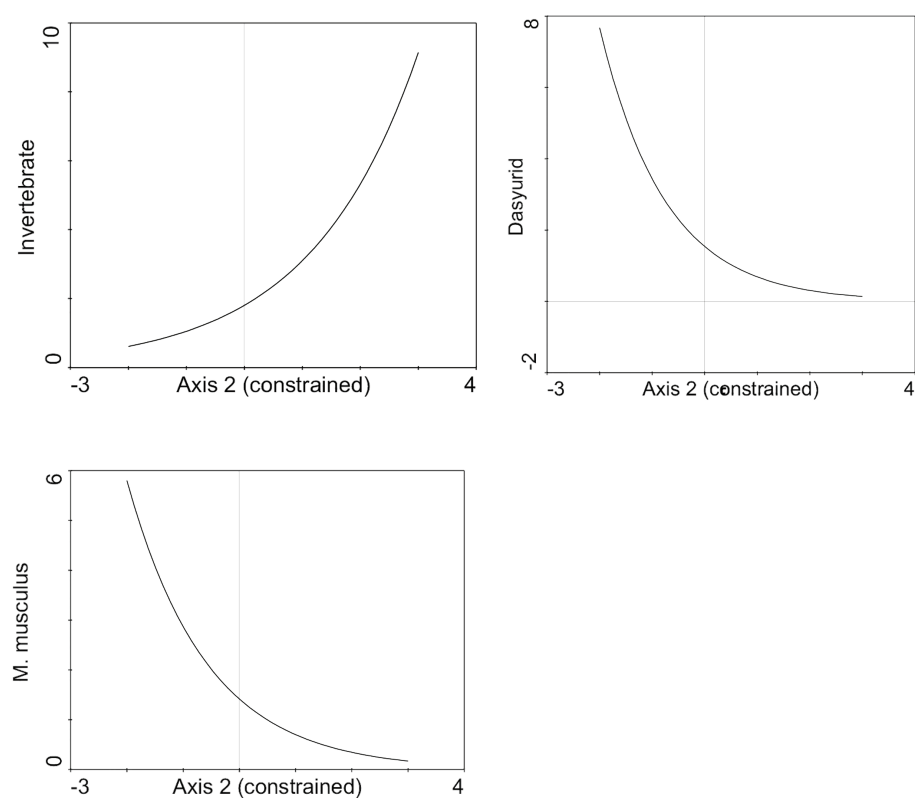
APPENDIX A

Species response curve of prey groups in red fox scats along the first axis (a) and second axis (b) showing prey groups that had significant relationships with each axis ($p \leq 0.05$) fitted using GLMs.

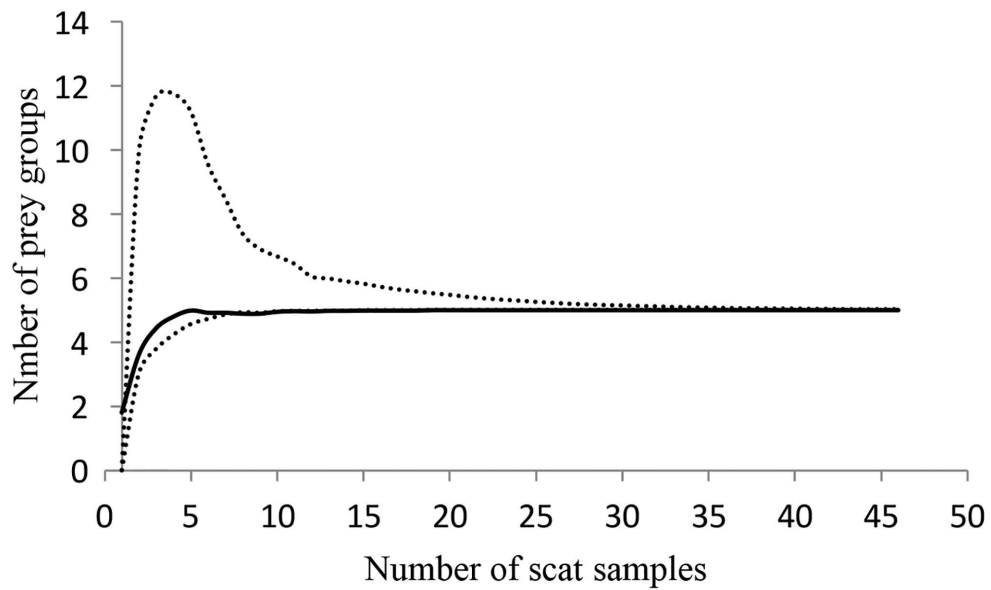
a).



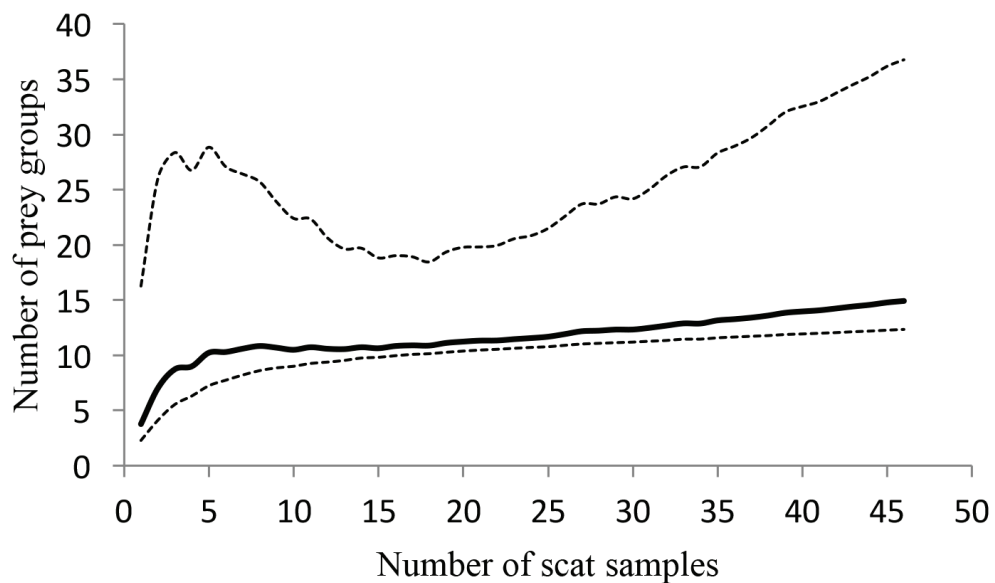
b).



APPENDIX B

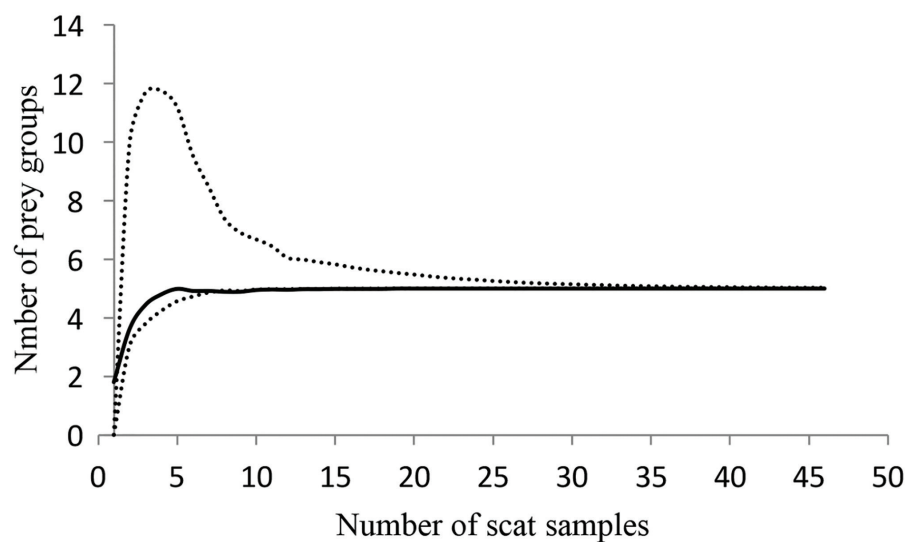
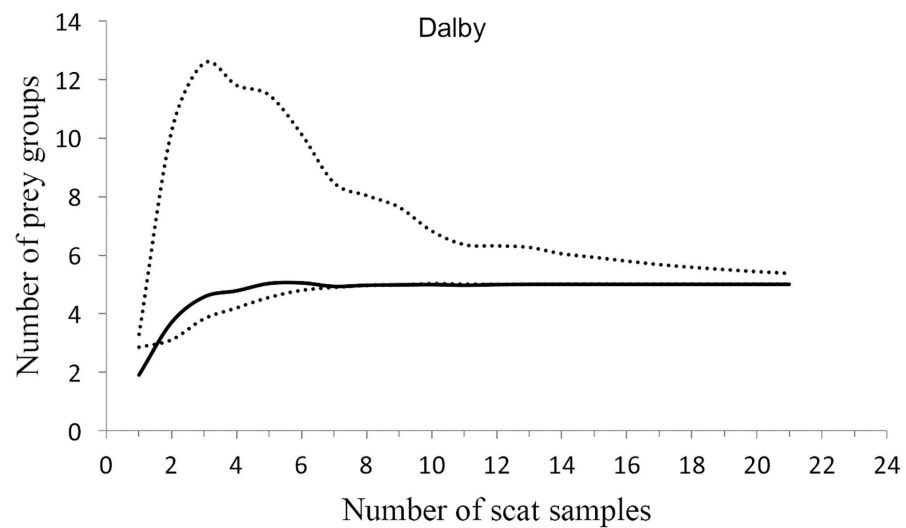
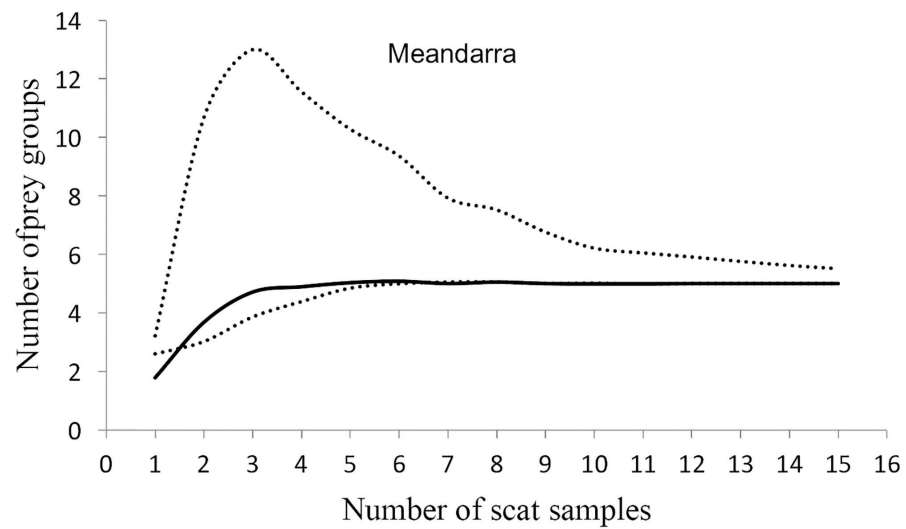


B.1. Sample-based rarefaction curve at the regional level of prey that contributed >5% mass to the total scat mass (solid line) with upper and lower 95% unconditional confidence interval (dashed lines). Curve reaches an asymptote at 16 scat samples and the unconditional confidence interval envelope closes indicating adequacy of sample size for representing the diet of red foxes.



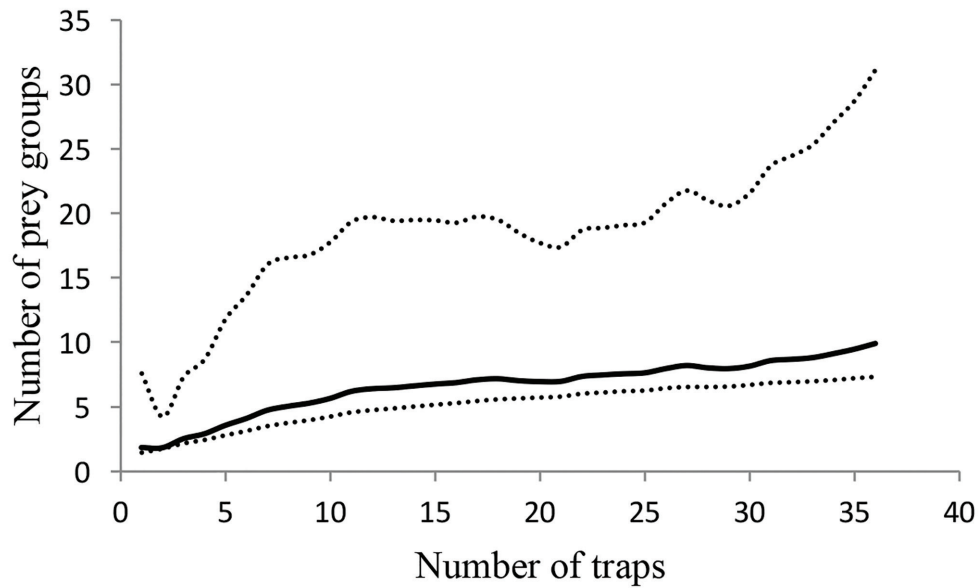
B.2. Sample-based rarefaction curve of all prey among scats (solid line) with upper and lower 95% unconditional confidence interval (dashed lines). The sample-based rarefaction curve does not reach an asymptote nor does the unconditional confidence interval envelope close indicating the sample size is inadequate at a regional level when including incidental prey items.

APPENDIX B

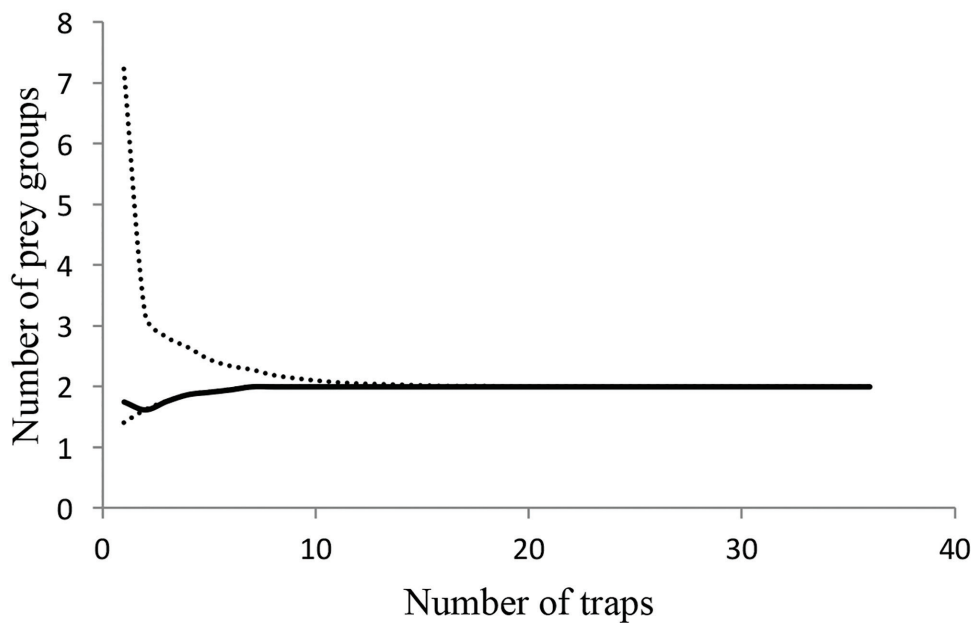


B.3. Sample-based rarefaction curve at the sub-regional level of prey that contributed >5% mass to the total scat mass (solid line) with upper and lower 95% unconditional confidence interval (dashed lines). Rarefaction curves reach an asymptote; however, the confidence interval envelopes do not close indicating low confidence in the data at a sub-regional level.

APPENDIX C

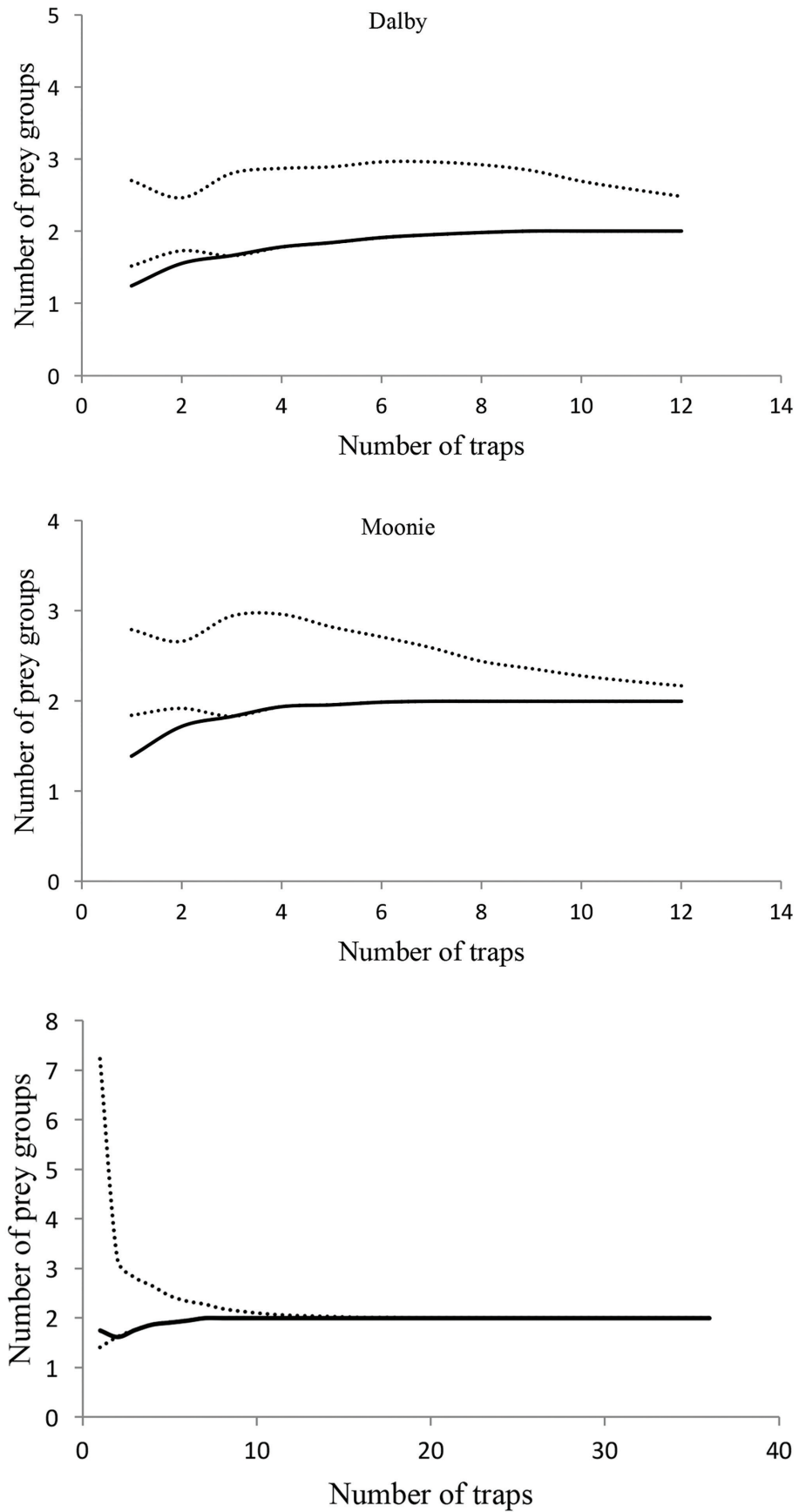


C.1. Sample-based rarefaction curve at the regional level of all prey species detected in small mammal surveys (solid line) with upper and lower 95% unconditional confidence interval (dashed lines). Rarefaction curve does not reach an asymptote and the confidence interval envelope fails to close indicating data is not suitable for analysis at a regional level and subsequently at a sub-regional level also.



C.3. Sample-based rarefaction curve at the sub-regional level of *M. musculus* and pooled *Sminthopsinae* (solid line) with upper and lower 95% unconditional confidence interval (dashed lines). Rarefaction curves reach an asymptote; however, the confidence interval envelopes do not close indicating low confidence in the data at a sub-regional level.

APPENDIX C



C.2. Sample-based rarefaction curve at the regional level of *M. musculus* and pooled *Sminthopsinae* (solid line) with upper and lower 95% unconditional confidence interval (dashed lines). Curve reaches an asymptote and the unconditional confidence interval envelope closes indicating adequacy of sample size for analysing small vertebrate prey data.